

Article



https://doi.org/10.11646/zootaxa.4779.4.3 http://zoobank.org/urn:lsid:zoobank.org:pub:FB9DEC58-77E7-4994-8918-C05278C949AA

A revision of Strigiphilus (Insecta: Phthiraptera: Philopteridae) from Japan

MEGUMI SHIMADA^{1,*} & KAZUNORI YOSHIZAWA^{1,2}

Systematic Entomology, Graduate School of Agriculture, Hokkaido University, Sapporo, 060-8589 Japan

² https://orcid.org/0000-0001-6170-4296

*Corresponding author. • meg.shimada.hdag@gmail.com; • https://orcid.org/0000-0002-6071-7682

Abstract

The Japanese species of the genus *Strigiphilus* Mjöberg, 1910 (Insecta: Phthiraptera: Philopteridae) are revised. Six species are recorded, including a new species belonging to the *cursitans* species-group: *Strigiphilus stenocephalus* **new species**, described from the type host *Otus bakkamoena semitorques* and based on specimens originally identified and reported by Uchida (1949) as *Strigiphilus rostratus* (Burmeister, 1838). A lectotype for *Strigiphilus laticephalus* (Uchida, 1949) (type host: *Strix aluco yamadae*) is designated and redescribed, and this louse species is synonymized under *Strigiphilus cursor* (Burmeister, 1838). *Strigiphilus ceblebrachys* (Denny, 1842), *S. heterogenitalis* Emerson & Elbel, 1957 and *S. tuleskovi* Balát, 1958 are recorded for the first time in Japan. Also, *Strix uralensis* and *Otus sunia japonicus* are recorded as new hosts for *Strigiphilus heterogenitalis* and *S. tuleskovi* respectively.

Key words: Chewing lice, Phthiraptera Philopteridae, *Strigiphilus*, Japan, key to species, new synonymy, redescription

Introduction

Chewing lice are obligate parasites which spend their entire life cycle on the host (Price *et al.* 2003). Therefore, extensive host-parasite co-speciation is expected (*e.g.* Hafner *et al.* 1994; Page *et al.* 1998; Hughes *et al.* 2007). However, as noted by Clay (1966a,b) and Clayton (1990), several species of *Strigiphilus* are known to parasitise each a wide range of hosts. Therefore, more data on the host-parasite associations of *Strigiphilus* species are useful to understand the ecological parameters that govern congruence or incongruence in the relationship between owls and their lice (*e.g.* Johnson *et al.* 2002).

The genus *Strigiphilus* Mjöberg, 1910 (Phthiraptera: Philopteridae: *Philopterus*-complex *sensu* Smith 2001) comprises chewing lice that exclusively parasitise owls (Aves: Strigiformes). Currently, about 46 species are recognised as valid (Price *et al.* 2003) from all the zoogeographical regions, of which four have been recorded from Japan (Uchida 1948, 1949).

All species of Japanese *Strigiphilus* were described or recorded by Uchida (1948, 1949), but he did not include figures of their male genitalia and gave little or no information about them, making some of his identifications doubtful. For example, Uchida (1949: 542) recorded *Strigiphilus rostratus* (Burmeister, 1838) [as "*Philopterus rostratus* (Nitzsch)"] from *Otus bakkamoena semitorques* Temminck & Schlegel, 1844 (Strigidae), but this chewing louse species is only known to parasitise barn owls, *Tyto alba* (Scopoli, 1759) (Tytonidae; see Clay 1966a). Since Uchida's (1948, 1949) reports, no additional studies of Japanese *Strigiphilus* have been published.

In this paper, we provide the results of a systematic review of the species of *Strigiphilus* from Japan, based on Uchida's collection and additional specimens collected from *Bubo scandiacus* (Linnaeus, 1758), *Strix uralensis* Pallas, 1771, *Ninox scutulata* (Raffles, 1822), *Otus sunia japonicus* (Temminck & Schlegel, 1844) and *Otus lempiji pryeri* (Gurney, 1889). We describe and name one new species, synonymise another species, and record three other species for the first time, bringing the total of known Japanese species of *Strigiphilus* to six, belonging to four species-groups. Also, we provide a key for their identification and we discuss the host-parasite relationships between Japanese species of *Strigiphilus* and their owl hosts.

Materials and methods

The lice of the Uchida collection were in poor condition because some types and all non-types examined had been originally preserved in ethanol, which had completely dried up, causing the lice to glue onto the inner surface of the vials. Those specimens were soaked with 80% ethanol for one day, then removed from the vials using a fine brush, and stored in 80% ethanol. All samples included a label with information handwritten by Uchida, which was very useful to recognise the types and other specimens he examined. Subsequently, most of the type specimens and some non-types were slide-mounted by us for the purpose of this survey. We attached new labels to the slide-mounted specimens, following the same format from Uchida's label, with numbers within parentheses indicating separation of labels. In the lists of specimens examined under each species below, a slash (/) indicates separation of lines on slide labels, and data written in Japanese letters (Kanji or Katakana) are indicated within square brackets.

We also examined specimens preserved in ethanol 99%, borrowed from the Yamashina Institute for Ornithology, Chiba, Japan. Specimens in ethanol were first soaked with 10% KOH solution at room temperature for one night, then rinsed with 80% ethanol, passed through a series of ethanol at higher concentrations to dehydrate them, and slide-mounted in Euparal.

Morphological data was mainly taken from slide-mounted specimens, using a Leica TCS SP5 confocal microscope (Leica Microsystems GmbH, Wetzlar, Germany) and a Zeiss Axiophot microscope (Carl ZeissAG, Jena, Germany). Photographs were taken with an AxioCam ERc 5s (Carl ZeissAG, Jena, Germany). Image J (U.S. National Institutes of Health, Bethesda, Maryland, U.S.A.) was used to take measurements. The final images were prepared with Photoshop CC2018 and Illustrator CC2018 (Adobe Inc., San Jose, California, U.S.A.).

We followed Clay (1966b) and Clayton & Price (1984) for the subdivision of the genus *Strigiphilus* into species-groups, and the Ornithological Society of Japan (2012) for the names of owl species.

Abbreviations (see Fig. 1): AHW, anterior head width; AW, abdominal width at segment V; CL, conus length; DAPW, dorsal anterior plate width; DAPL, dorsal anterior plate length; GW, male genitalia width; GL, male genitalia length; HL, head length; MW, metathorax width; PCHW, preconal head width; PW, prothorax width; SGPW female subgenital plate width; TL, total body length; TW, temple width.

Repositories of specimens

ELKU—Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka, Japan.

NMHL—Natural History Museum, London, United Kingdom.

SEHU—Insect Collection, Hokkaido University, Sapporo, Hokkaido, Japan.

YIO—Yamashina Institute for Ornithology, Abiko, Chiba, Japan.

Systematics

Phthiraptera Haeckel, 1896

Ischnocera Kellogg, 1896

Philopteridae Burmeister, 1838

Strigiphilus Mjöberg, 1910

The heterocerus species-group

Diagnosis. (1) Abdominal tergite III with postspiracular setae; (2) metanotum with 3–4 long, 1 medium and 1 very short posterolateral setae on each side; and (3) male genitalia as in Fig. 4, with a thickened central prolongation of basal apodeme (see Clay 1966b: fig. 14).

Here, we record one species of the *heterocerus* species-group from Japan: *Strigiphilus heterocerus* (Grube, 1851), previously reported by Uchida (1948) as "*Strigiphilus fukuro* n. sp."

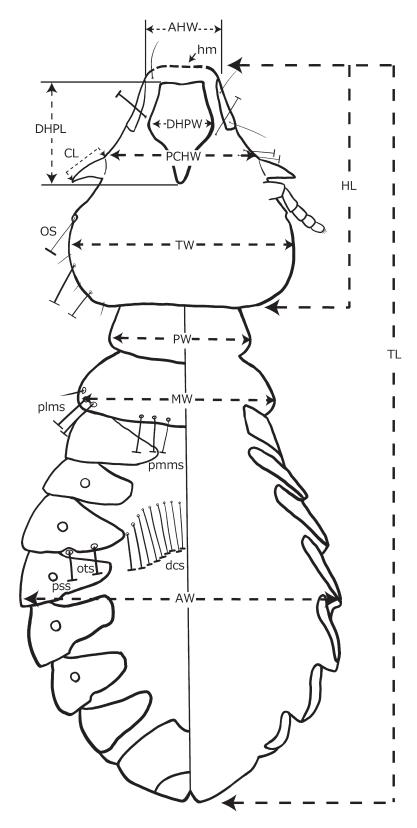


FIGURE 1. Strigiphilus. Schematic dorsal-ventral view of a female showing measurements, some features and setal nomenclature. Abbreviations: AHW, anterior head width; AW, abdominal width at segment V; CL, conus length; dcs, dorsal central setae of abdominal segment IV; DAPL, dorsal anterior plate length; DAPW, dorsal anterior plate width; HL, head length; hm, hyaline margin; MW, metathorax width; OS, ocular seta; ots, outer tergal seta of abdominal segment IV; PCHW, preconal head width; plms, posterolateral metanotal setae; pmms, posteromedial metanotal setae; pss, postspiracular seta of segment IV; PW, prothorax width; TL, total body length; TW, temple width.

Strigiphilus heterocerus (Grube, 1851)

(Figs 2-6)

Docophorus heterocerus Grube, 1851: 469.

Type host: Strix uralensis liturata (Tengmalm, 1795).

Strigiphilus fukuro Uchida, 1948: 307, fig.1; Hopkins & Clay 1952: 339.

Type host: Strix uralensis hondoensis (Clark, 1907).

Neodocophorus uralensis Eichler, 1949: 15, figs 33–34; Hopkins & Clay 1952: 340.

Type host: Strix uralensis liturata (Tengmalm, 1795).

Strigiphilus heterocerus (Grube, 1851): Hopkins & Clay, 1952: 339.

Diagnosis. Among the Japanese species of *Strigiphilus*, this species is easily identified by (1) a short preconal area of the head with anterior margin slightly concave (Figs 2, 5), (2) sexually dimorphic antennae (Figs 2, 5), (3) the shape of dorsal anterior plates (Figs 3, 6), and (4) the morphology of the male genitalia (Fig. 4).

Material examined. Type specimens. Ex Strix uralensis hondoensis: Syntypes of Strigiphilus fukuro: 1♂ (slide-mounted), Fukuro [= Strix uralensis hondoensis, in Katakana], Nagano Prefecture [in Kanji], Japan, 24 Dec. 1916 (ELKU); 2♂, 5♀, 9N (preserved in alcohol) same data (ELKU). Slide-mounted syntypes are labeled as "(1) Syntype/ Strigiphilus fukuro/ Uchida, 1948/ det. Shimada & Yoshi, 2020; (2) Nagano Pref./ (24. xii. 1916)/ ex Strix uralensis" (ELKU); 1♀ (slide-mounted #010693510) (1) "Strigiphilus fukuro Uchida, 1948/T. Clay det./ PARA-TYPE" [no holotype designation was made in the original description by Uchida (1948), therefore this specimen is actually a syntype]. (2) "Strigiphilus fukuro n. sp./ Fukuro [in Katakana]/ Shinshu [in Kanji = Nagano Prefecture] 33" (NMHL). Data taken from NHML online database accessed on 23 Apr. 2020—https://data.nhm.ac.uk

Non-type specimens. Ex *Strix uralensis spp.*: $23 \circlearrowleft$, $48 \circlearrowleft$, 1N (slide-mounted) Amakubo, Tsukuba City, Ibaraki Prefecture, Japan, 9 Feb. 2009, Haruhiko Asuka & Miyako Tsurumi (SEHU); $26 \circlearrowleft$, $89 \circlearrowleft$, 40 N (preserved in alcohol) same data (YIO); $1 \circlearrowleft$, $1 \hookrightarrow$ (slide-mounted), Bibi, Chitose City, Hokkaido, Japan, 10 Mar. 2006, Miyako Tsurumi (SEHU); $4 \circlearrowleft$, $18 \hookrightarrow$, 23 N (preserved in alcohol) same data (YIO).

Japanese host: Strix uralensis hondoensis (Clark, 1907).

Other hosts. Strix uralensis uralensis Pallas, 1771, Strix uralensis liturata (Tengmalm, 1795).

The cursor species-group

Diagnosis. (1) Abdominal tergite III with postspiracular setae, (2) metanotum with 2 long and 1 medium posterolateral setae on each side, and (3) male genitalia without thickened central prolongation of basal apodeme (Figs 9, 14).

Here, we record one species of the *cursor* species-group from Japanese hosts: *Strigiphilus cursor* (Burmeister, 1838). Uchida (1949) recorded specimens of this species as "*Philopterus cursor*" and as "*Philopterus cursor* var *laticephalus*" (see below).

Strigiphilus cursor (Burmeister, 1838)

(Figs 7–16)

Docophorus cursor Burmeister, 1838: 426.

Type host: Asio flammeus flammeus (Pontoppidan, 1763).

Nirmus brachyoti Denny, 1852: 13; Hopkins & Clay 1952: 338.

Type host: Asio flammeus flammeus (Pontoppidan, 1763).

Nirmus stridulae Denny, 1852: 13; Hopkins & Clay 1952: 340.

Type host: Asio flammeus flammeus (Pontoppidan, 1763).

Docophorus nudipes Piaget, 1880: 26, pl. I, fig.6; Clay 1966b: 844.

Type host: Asio flammeus flammeus (Pontoppidan, 1763).

Philopterus cursor Nitzsch in Burmeister, 1838: Uchida, 1949: 542.

[&]quot;Strigiphilus laticephalus Złotorzycka, 1974: 324, fig. 48". Not Philopterus cursor var laticephalus Uchida, 1949.

[&]quot;Strigiphilus laticephalus Adam & Daróczi, 2006: 157, figs 11c,d". Not *Philopterus cursor* var laticephalus Uchida, 1949. Strigiphilus heterocerus (Grube, 1851): Price et al. 2003: 239.

Philopterus cursor var laticephalus Uchida, 1949: 543 [in part]. New synonymy.

Type host: Strix aluco yamadae Yamashina, 1936.

Strigiphilus cursor (Burmeister, 1938): Hopkins & Clay, 1952: 339.

Strigiphilus laticephalus (Uchida, 1949): Hopkins & Clay, 1952: 340.

Strigiphilus nudipes (Piaget, 1880); Hopkins & Clay 1952: 340.

Strigiphilus cursor (Burmeister, 1938); Price et al. 2003: 239.

Diagnosis. *Strigiphilus cursor* can be distinguished from other species of Japanese *Strigiphilus* by the following characters (1) abdominal tergite III with postspiracular setae, (2) the metanotum with 2 long and 1 medium posterolateral setae on each side, (3) the shape of dorsal anterior plates (Figs 8, 11, 13, 16), and (4) the morphology of the male genitalia (Figs 9, 14).

Material examined. Type specimens. Ex Strix aluco yamadae: Lectotype ♂ (here designated) of Philopterus cursor laticephalus Uchida, 1949. Originally labeled as "Philopterus cursor laticephalus n. var./ Takasago-fukuro [= Strix aluco yamadae: in Katakana], Ishigakijima [in Kanji], 18. XII. 1924" (ELKU). Paralectotypes: 4♂, 13♀, with same data as lectotype (ELKU). The lectotype and 4♂, 7♀ paralectotypes are slide-mounted, and labeled as "(1) (Para) Lectotype/ Philopterus cursor/ var laticephalus/ Uchida, 1949; (2) Strigiphilus cursor/ det. Shimada & Yoshi, 2020; (3) Ishigakijima/ Ryukyus/ 18. xii. 1924/ ex. Strix aluco yamadae".

Note: There is a discrepancy on the year of collection of the above-listed specimens, being "1923" in Uchida (1949: 543), but "1924" in Uchida's label attached to the lice. However, as all other label data are in complete agreement with the data given by Uchida (1949: 543), we concluded that these specimens are those examined by Uchida (1949) and published as "*Philopterus cursor* var *laticephalus* n. var.".

Non-type specimens. Ex *Asio flammeus flammeus*: $1 \circlearrowleft , 2 \circlearrowleft , 1$ N (slide-mounted), originally labeled as "*Philopterus cursor* N./ Komimizuku [= *Asio flammeus flammeus*: in Katakana], Chiba Prefecture Funabashi [in Kanji], 14. XII. 1924" (ELKU); 1N (preserved in alcohol) same data (ELKU). Ex *Asio flammeus* ssp.: $1 \circlearrowleft$ (slide-mounted), Fukuei, Ichikawa City, Chiba Prefecture, Japan, 29 Aug. 2006, Tatsuo Sato (SEHU); $1 \circlearrowleft$ (preserved in alcohol) same data (YIO); $1 \circlearrowleft$ (slide-mounted), Takarajima, Toshima Village, Kagoshima Prefecture, Japan, 3 Dec. 2007, Isao Nishiumi & Yasuko Iwami (SEHU).

Japanese hosts: *Strix aluco yamadae* Yamashina, 1936, *Asio flammeus flammeus* (Pontoppidan, 1763). **Other hosts.** *Asio flammeus* sspp.

Redescription of lectotype and paralectotypes of "Philopterus cursor var laticephalus"

Male as in Fig. 12. Head short and rounded, cephalic index (CI) = 0.868–0.961, preconal head margin concave; dorsal anterior plate (Fig. 13) longer than wide and approximately two-fifth the length of head; hyaline margin with long lateral seta on each side; anterodorsal head margin with a long seta on each side, anteroventral head margin with 1 long and 2 short setae on each side; ventral preconal head margin with 2 long setae on each side; ocular seta long; temple with 2 long and 3 very short setae on each side. Prothorax trapezoidal, pronotum with a long posterolateral seta on each side; prosternum with 2 long and 2 short setae; metanotum with 2 long and 1 medium posterolateral setae on each side, 8-11 medium to long posteromedial setae; mesosternum with 3 medium setae; metasternum with 4-6 medium setae. Abdominal chaetotaxy: segments III-VII with a long postspiracular seta, abdominal segments II–VIII with a long outer tergal seta; tergocentral setae of abdominal segments: II, 11–13; III, 11–17; IV, 14–16; V, 10–15; VI, 9–13; VII, 6–9; VIII, 7–8; ventral setae of abdominal segments: II, 5–13; III, 17–19; IV, 17–20; V, 15–18; VI, 11–14; VII, 2; VIII, 0; pleural setae of abdominal segments, on each side: II, 0; III, 1; IV, 4; V, 4; VI, 3–5; VII, 3-4; VIII, 4; terminal segment of abdomen with 2-3 long anteropleural setae on each side, ventral margin with 6-10 long setae, and dorsal margin with 11–13 long setae. Genitalia as in Fig. 14. Measurements (n=4, all in mm): DAPW 0.193-0.209; DAPL 0.282-0.321; CL 0.097-0.137; AHW 0.229-0.233; PCHW 0.450-0.485; TW 0.647-0.697; HL 0.725-0.750; PW 0.407-0.466; MW 0.591-0.630; AW 0.786-0.923; TL 2.047-2.055; GW 0.152-0.174; GL 0.496 - 0.659.

Female as in Fig. 15. Head (CI = 0.824–0.957), dorsal anterior plate as in Fig. 16. Thorax as in male. Abdominal chaetotaxy: tergocentral setae on segments: II, 8–13; III, 14–15; IV, 14–17; V, 17–18; VI, 12–17; VII, 9–12; VIII, 6–8. Ventral setae on segments: II, 10–14; III, 15–17; IV, 13–17; V,13–20; VI, 12–18; VII, 4; VIII, 0. Pleural setae on each side of segments: II, 0; III, 1; IV, 3–4; V, 4; VI, 4–5; VII, 3–5; VIII, 3–4. Terminal segment: 2–3 long antero-

pleural setae on each side, posteroventral margin with 6–7 long setae on each side, dorsal margin with 2–4 long and 0–2 very short setae. *Measurements* (n=4, all in mm): DAPW 0.210–0.225; DAPL 0.303–0.341; CL 0.125–0.138; AHW 0.238–0.263; PCHW 0.488–0.522; TW 0.655–0.761; HL 0.760–0.795; PW 0.420–0.451; MW 0.612–0.642; AW 0.856–0.976; TL 2.216–2.318; SGPW 0.378–0.437.

Male of *Strigiphilus cursor* (for comparisons with *S. laticephalus*): *Abdominal chaetotaxy*: Segments III–VII with a long postspiracular seta, abdominal segments II–VIII with a long outer tergal seta; tergocentral setae of abdominal segments: II, 12; III, 15; IV, 19; V, 16; VI, 12; VII, 10; VIII, 9; ventral setae of abdominal segments: II, 13; III, 19; IV, 15; V, 17; VI, 17; VII, 2; VIII, 0; pleural setae of abdominal segments, on each side: II, 0; III, 1; IV, 4; V, 4; VI, 5; VII, 4; VIII, 3; terminal segment of abdomen with 2 long anteropleural setae on each side, ventral margin with 6 long setae, and dorsal margin with 12 long setae.

Female of Strigiphilus cursor (for comparisons with S. laticephalus): Tergocentral setae on segments: II, 12–14; III, 14–18; IV, 15–20; V, 16–17; VI, 13–14; VII, 11–14; VIII, 6–8. Ventral setae on segments: II, 8–13; III, 15–19; IV, 17–19; V,15–17; VI, 14–17; VII, 4; VIII, 0. Pleural setae on each side of segments: II, 0; III, 1; IV, 3–4; V, 4; VI, 4–5; VII, 3–5; VIII, 3–4. Terminal segment: 2–3 long anteropleural setae on each side, posteroventral margin with 7–10 long setae on each side, dorsal margin with 2–4 long setae.

Remarks. Up to now, two species of the *cursor* species-group were recognised from Japan: *Strigiphilus cursor* (Burmeister, 1938) and *Strigiphilus laticephalus* (Uchida, 1949) (Price *et al.* 2003). Clay (1966b: 843) placed *S. laticephalus* in the *heterocerus* species-group without any comment, probably because of its host association with *Strix uralensis*, which is also the type host of *S. heterocerus*. Złotorzycka (1974: 324, figs 4–8, 48) identified lice from *Strix aluco aluco* as *S. laticephalus*. However, judging from Złotorzycka's (1974) description and illustrations, her specimens appear to be members of the *heterocerus* species-group and, therefore, cannot be conspecific with Uchida's *S. laticephalus*. Similarly, Adam & Daróczi (2006: 157, figs 11c,d) identified as *S. laticephalus* specimens from *Strix aluco* but, again, their figures show that they belong to the *heterocerus* species-group.

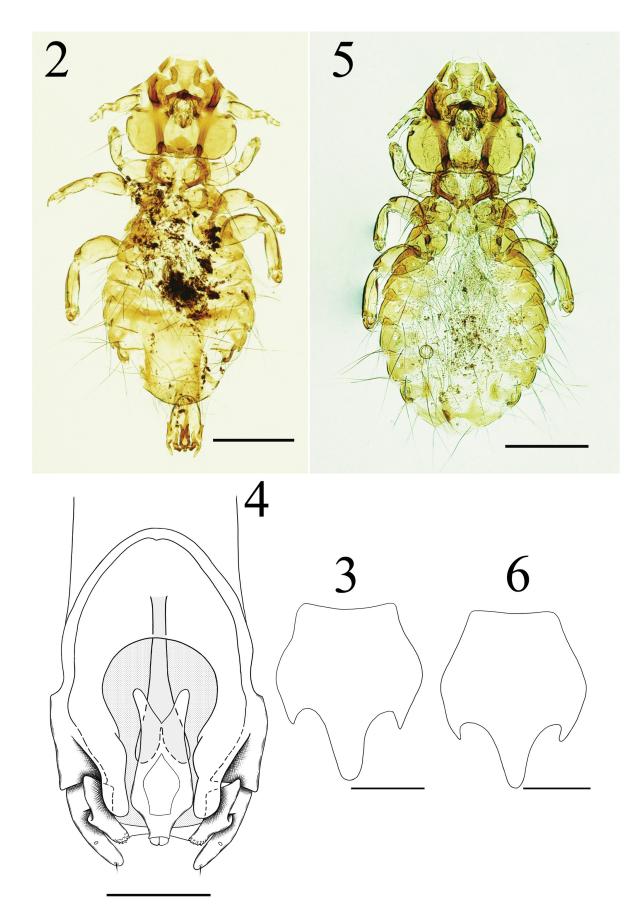
Our examination of Uchida's material revealed that the syntype series of *Philopterus cursor laticephalus* included two different louse species from two different hosts, one belonging to the *cursor* species-group and the other to the *macrogenitalis* species-group. Therefore, in this paper we designate a male specimen from *Strix aluco yamadae* as the lectotype of *Philopterus cursor laticephalus*, which becomes a junior subjective synonym of *Strigiphilus cursor*. Furthermore, the remaining paralectotypes of *Philopterus cursor laticephalus* from *Strix uralensis fuscescens* are conspecific with *Strigiphilus heterogenitalis* Emerson & Elbel, 1957 (see below).

In the original description, Uchida (1949: 543) noted that the head of *Strigiphilus laticephalus* is wider than that of *S. cursor*, hence the name "*laticephalus*", meaning "wide head". However, our examination clearly showed that the heads of the syntypes from *Strix aluco yamadae*—now the lectotype and paralectotype series of *S. laticephalus*—are not as wide as described by Uchida (1949), who measured them from wet specimens. Furthermore, our comparison of these types against other specimens of *S. cursor* showed that the characters used by Uchida (1949) to separate *S. laticephalus* from *S. cursor* follow a continuous range of variation (Figs 7–8, 10–13, 15–16). We also compared the abdominal chaetotaxy of both sexes of *S. laticephalus* with those of *S. cursor* (see details above), and their ranges largely overlapped. Differences between the male genitalia of these two nominal species are also minor and should be interpreted as intraspecific variation (Figs 9, 14). Therefore, *Philopterus cursor laticephalus* is here regarded as a subjective junior synonym of *Strigiphilus cursor*.

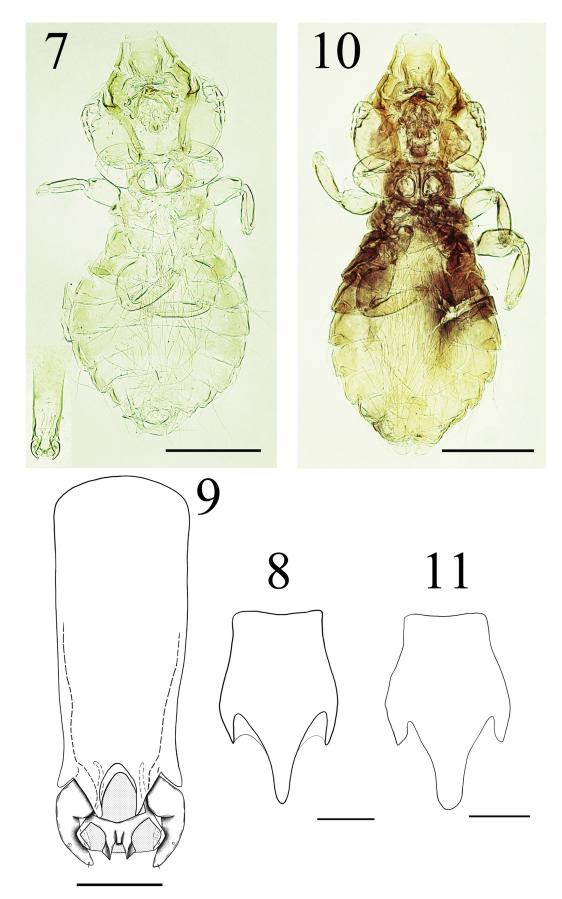
The *macrogenitalis* species-group

Diagnosis. (1) Abdominal tergite III without postspiracular seta, (2) male tergite VII continuous across the segment, and (3) male genitalia with enlarged mesosome separated from basal apodeme, and without central prolongation (Figs 19, 24, 28).

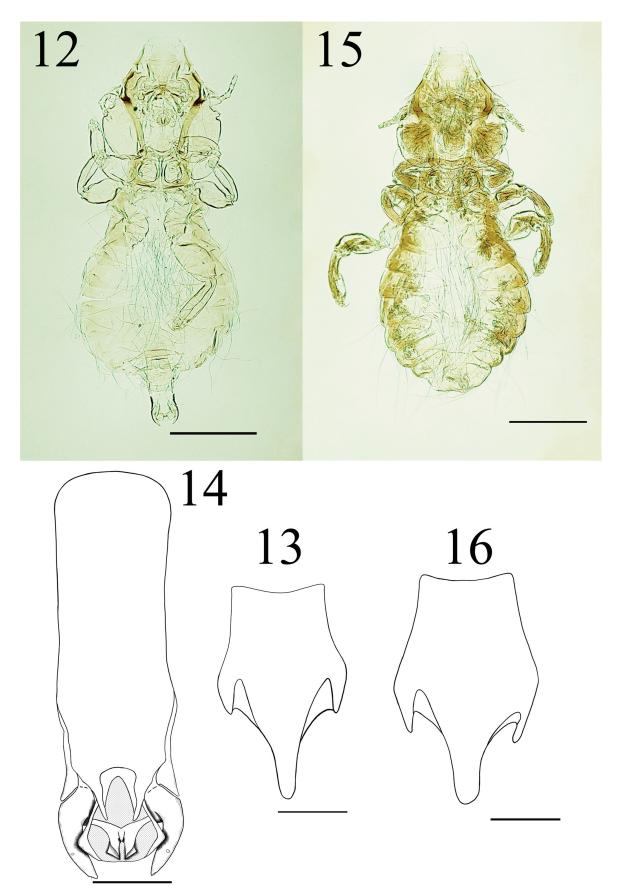
Here we record one species of the *macrogenitalis* species-group from Japanese hosts: *Strigiphilus heterogenitalis* Emerson & Elbel, 1957. This is a new species record for Japan.



FIGURES 2–6. *Strigiphilus heterocerus*: **2**, male habitus. **3**, male dorsal anterior plate. **4**, male genitalia. **5**, female habitus. **6**, female dorsal anterior plate. Scale bar for **2** and **5**: 0.5mm; for **3**, **4** and **6**: 0.1mm.



FIGURES 7–11. *Strigiphilus cursor* [specimens identified by Uchida (1949: 542) as "*Philopterus cursor*" from *Asio flammeus flammeus*]: **7**, male habitus. **8**, male dorsal anterior plate. **9**, male genitalia. **10**, female habitus. **11**, female dorsal anterior plate. Scale bar for **7** and **10**: 0.5mm; for **8**, **9** and **11**: 0.1mm.



FIGURES 12–16. *Strigiphilus cursor* [specimens identified by Uchida (1949: 543) as "*Philopterus cursor* var *laticephalus*" from *Strix aluco yamadae*]: **12**, male habitus. **13**, male dorsal anterior plate. **14**, male genitalia. **15**, female habitus. **16**, female dorsal anterior plate. Scale bar for **12** and **15**: 0.5mm; for **13**, **14** and **16**: 0.1mm.

Strigiphilus heterogenitalis Emerson & Elbel, 1957 (Figs 17–29)

"Philopterus cursor var laticephalus Uchida, 1949: 543". [in part]. Not *Docophorus cursor* Burmeister, 1938; not *Strigiphilus laticephalus* (Uchida, 1949). **New synonymy**.

Host: Strix uralensis fuscescens Temminck & Schlegel, 1850.

Strigiphilus heterogenitalis Emerson & Elbel, 1957: 198, figs 5, 10.

Type host: Otus bakkamoena lettia Hodgson, 1836.

Strigiphilus heterogenitalis Emerson & Elbel, 1957; Clay 1966b: 842.

Strigiphilus heterogenitalis Emerson & Elbel, 1957; Price et al. 2003: 239.

Diagnosis. *Strigiphilus heterogenitalis* can be distinguished from other Japanese species by the following characters (1) its long dorsal anterior plate relative to head length, with DAPL/HL about 0.5 (Figs 17, 20, 22, 25 27), (2) the shape of dorsal anterior plates (Figs 18, 21, 23, 26, 29), and (3) the morphology of the male genitalia (Figs 19, 24, 28).

Material examined. Type specimens. Ex Strix uralensis fuscescens: 1♂, 3♀, paralectotypes of Philopterus cursor laticephalus (ELKU), originally labeled as "Philopterus cursor laticephalus n. var./ Kiushiu-fukuro [= Strix uralensis fuscescens: in Katakana], Kagoshima Prefecture [in Kanji], 10. III. 1911". Some paralectotypes are slidemounted and labeled as "(1) Syntype/ Strigiphilus cursor/ var laticephalus/ Uchida, 1949; (2) Strigiphilus heterogenitalis/ det Shimada & Yoshi, 2020; (3) Kagoshima Pref./ 10. iii. 1911/ ex. Strix uralensis fuscescens".

Non-type specimens. Ex *Ninox scutulata*: $4\colone{0}$, $4\colone{0}$, (slide-mounted), Nago City, Okinawa Prefecture, Japan, 9 Jan. 2011, Ichiro Kikuta (SEHU); $2\colone{0}$, $6\colone{0}$, 1N (preserved in alcohol), same data (YIO). Ex *Otus lempiji pryeri*: $3\colone{0}$, $2\colone{0}$ (slide-mounted), Ôgimi Village, Okinawa Prefecture, Japan, 1 Jan. 2012, Yutaka Tokuchi (SEHU); $3\colone{0}$, $12\colone{0}$, 2N (preserved in alcohol), same data (YIO); $2\colone{0}$ (slide-mounted), Kunigami Village, Okinawa Prefecture, Japan, 8 Mar 2007, Hiroshi Shichiri (SEHU); $2\colone{0}$ (preserved in alcohol), same data (SEHU). Ex *Otus lempiji* ssp.: $1\colone{0}$, $1\colone{0}$, $1\colone{0}$, Okinawa Island, Okinawa Prefecture, Japan, 18 May 2010, Conservation & Animal Welfare Trust (SEHU); $1\colone{0}$, $7\colone{0}$ (preserved in alcohol), same data (SEHU).

Japanese hosts: *Ninox scutulata* (Raffles, 1822), *Otus lempiji pryeri* (Gurney, 1889) (**new host association**), *Otus lempiji* ssp., *Strix uralensis fuscescens* Temminck & Schlegel, 1850 (**new host association**).

Other hosts. Asio madagascariensis (A. Smith, 1834), Glaucidium brodiei (Burton, 1836), Ninox philippensis Bonaparte, 1855, Otus bakkamoena lettia, Otus manadensis (Quoy & Gaimard, 1830), Otus scops (Linnaeus, 1758), Otus spilocephalus (Blyth, 1846), Uroglaux dimorpha (Salvadori, 1874) (Price et al. 2003: 239).

Remarks. As discussed above under *Strigiphilus cursor*, the syntype series of *Philopterus cursor laticephalus* Uchida, 1949 contains two different species. Specimens of the second species belong to the *macrogenitalis* speciesgroup and are here identified as *S. heterogenitalis*. The publication date of *S. laticephalus* is earlier than that of *S. heterogenitalis* but, because the lectotype of *S. laticephalus* was selected from specimens conspecific with *S. cursor*, the name *S. heterogenitalis* is retained as valid.

The cursitans species-group

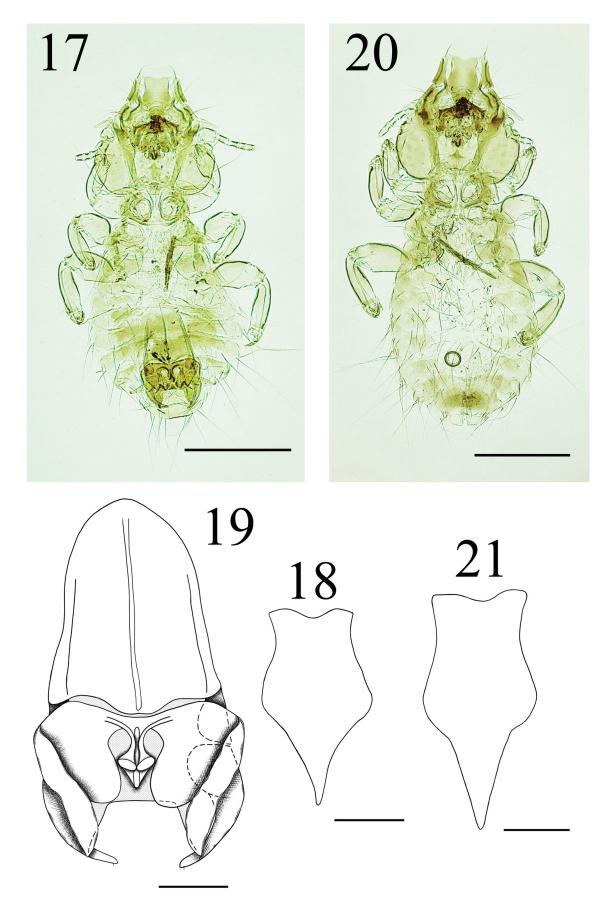
Diagnosis. (1) Absence of postspiracular seta on abdominal tergite III, (2) male tergites divided, and (3) basal apodeme of male genitalia with a forked prolongation, not fused to penis (Figs 32, 37, 42).

We have identified material of three species of the *cursitans* species-group parasitising Japanese hosts, as follows:

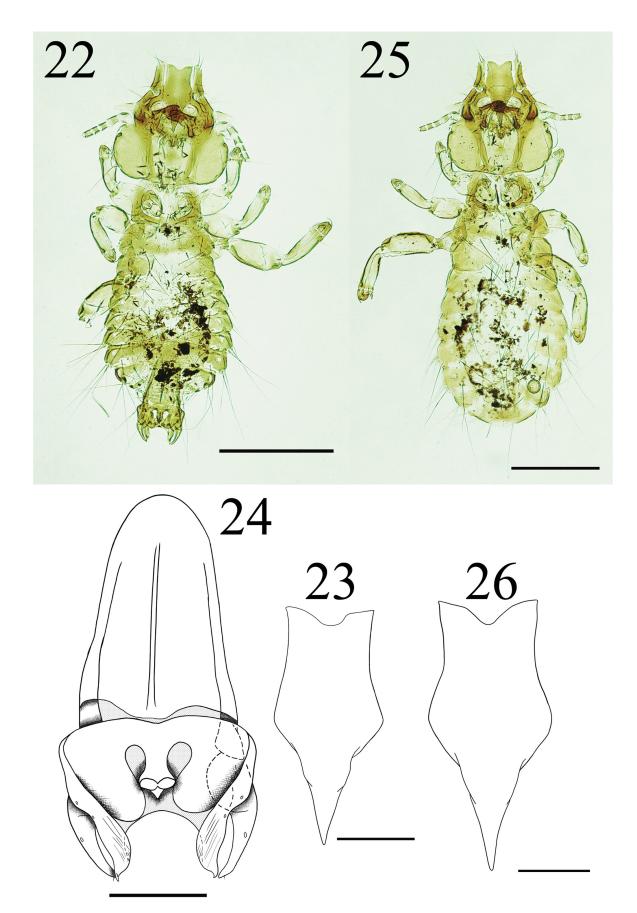
Strigiphilus ceblebrachys (Denny, 1842). New species record for Japan.

Strigiphilus stenocephalus new species.

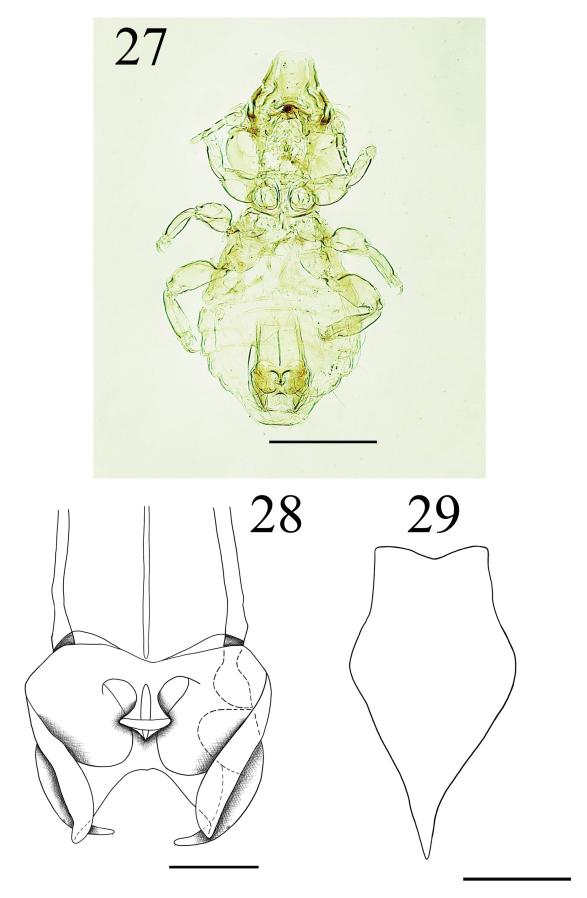
Strigiphilus tuleskovi Balát, 1958. New species record for Japan.



FIGURES 17–21. Strigiphilus heterogenitalis from Otus lempiji pryeri: 17, male habitus. 18, male dorsal anterior plate. 19, male genitalia. 20, female habitus. 21, female dorsal anterior plate. Scale bar for 17 and 20: 0.5mm; for 18, 19 and 21: 0.1mm.



FIGURES 22–26. *Strigiphilus heterogenitalis* from *Ninox scutulata*: 22, male habitus. 23, male dorsal anterior plate. 24, male genitalia. 25, female habitus. 26, female dorsal anterior plate. Scale bar for 22 and 25: 0.5mm; for 23, 24 and 26: 0.1mm.



FIGURES 27–29. Male *Strigiphilus heterogenitalis* from *Strix uralensis fuscescens* (paralectotype of *S. laticephalus*): 27, habitus. 28, genitalia. 29, dorsal anterior plate. Scale bar for 27: 0.5mm; for 28 and 29: 0.1mm.

Strigiphilus ceblebrachys (Denny, 1842)

(Fig. 30-34)

"Pediculus strigis O. Fabricius, 1780: 216". Not Pediculus strigis Pontoppidan, 1763.

Type host: *Bubo scandiacus* (Linnaeus, 1758).

Docophorus ceblebrachys Denny, 1842: 45, 92, pl. V, fig. 3.

Type host: Bubo scandiacus (Linnaeus, 1758).

Strigiphilus ceblebrachys (Denny, 1842); Hopkins & Clay, 1952: 339.

Strigiphilus ceblebrachys (Denny, 1842); Clayton & Price 1984: 353, figs 21, 42, 63.

Strigiphilus ceblebrachys (Denny, 1842); Price et al. 2003: 239.

Diagnosis. This species is easily distinguished from the other species of Japanese *Strigiphilus* by (1) its rounded head with a convex preconal area (Figs 30, 33), (2) the shape of dorsal anterior plate (Figs 31, 34) and (3) the configuration of the male genitalia (Fig. 32).

Material examined. Ex *Bubo scandiacus*: 5♂, 5♀ (slide-mounted), Lake Kutcharo-ko, Hamatombetsu Town, Hokkaido, Japan, 20 Mar. 2015, Kan Konishi (SEHU); 119♂, 262♀, 82N (preserved in alcohol), same data (YIO).

Japanese host: Bubo scandiacus (Linnaeus, 1758).

Other hosts: None.

Strigiphilus stenocephalus new species

(Figs 35-39)

Type host: Otus bakkamoena semitorques Temminck & Schlegel, 1844.

Type locality: Aomori Prefecture, Japan.

Diagnosis. *Strigiphilus stenocephalus* is similar to *S. tuleskovi* but it can be distinguished by (1) its larger head (male: HL > 0.58, TW > 0.46; female: HL > 0.6, TW > 0.5), (2) shorter male genitalia compared with total body length (Figs 35, 40), and (3) the configuration of the mesosome of the male genitalia, in particular the shape of the dorsal genitalic plate (Figs 37, 42; see also Clayton & Price 1984, fig. 56).

Material examined. Holotype \circlearrowleft : Ex *Otus bakkamoena semitorques*: Originally labeled as "*Strigiphilus*/ Ookonohazuku, (Tsukurimichi) Wada [in Kanji], 21. V. 1924" (ELKU). **Paratypes**: $1 \circlearrowleft$, $5 \circlearrowleft$, 1N, same data as for holotype (ELKU). All type specimens are now slide-mounted and labeled as (1) "Holo (Para) type/ *Strigiphilus stenocephalus*/ Shimada & Yoshi, 2020"; (2) "Tsukurimichi, (Aomori City)/ Aomori Pref./ 21. v. 1924/ S. Uchida/ ex. *Otus bakkamoena semitorques*".

Description. *Male.* Head short and rounded, preconal head margin concave, CI = 0.807–0.861 (Fig.35); dorsal anterior plate longer than wide, approximately two–fifths of the head length (Figs 36, 39); hyaline margin with a long lateral seta on each side; anterodorsal head margin with a long seta on each side; anteroventral head margin with 1 long and 2 short setae on each side; ventral preconal head margin with 2 long setae on each side; ocular seta long; temple with 2 long and 3 very short setae on each side. Prothorax trapezoidal, pronotum with a long posterolateral seta on each side; prosternum with 2 long and 2 short setae on each side; metanotum with 2 long and 1 short posterolateral setae on each side, and 7 long posteromedial setae; mesosternum with 3 medium setae; metasternum with 3 medium setae. Abdominal segments IV–VII with a long postspiracular seta; abdominal segments II–VIII with a long outer tergal seta; dorsal central setae of abdominal segments: II, 11; III, 14; IV, 14; V, 15; VI, 19; VIII, 9; VIII, 4; ventral setae of abdominal segments: II, 12; III, 13; IV, 14; V, 11; VI, 7; VII, 2; VIII, 0; pleural setae of abdominal segments, on each side: II, 0; III, 0; IV, 1; V, 3; VI, 3; VII, 3; VIII, 4; terminal segment of abdomen with 2 long anteropleural setae on each side, the posteroventral margin with 9 long setae on each side, and the dorsal margin with 10 long and 6 short setae. Genitalia as in Fig. 37. *Measurements* (n=2, all in mm). DAPW 0.162–0.164; DAPL 0.238–0.251; CL 0.068–0.084; AHW 0.202–0.205; PCHW 0.370–0.384; TW 0.468–0.512; HL 0.580–0.595; PW 0.283–0.288; MW 0.425–0.435; AW 0.540 (n=1); TL 1.653 (n=1); GW 0.108–0.111; GL 0.264–0.301.

Female. As in Fig. 38. Head and thorax as for male, except as follows: CI = 0.811–0.855. Dorsal central setae of abdominal segments: II 8–13; III 14–16; IV 14–17; V 13–17; VI 11–13; VII 6–9; VIII 4–5; ventral setae of abdominal segments: II 4–10; III 12–15; IV 12–16; V 10–14; VI 7–13; VII 4; VIII 0; pleural setae of abdominal segment on each side: II 0; III 1–0; IV 1–3; V 3; VI 3–4; VIII 3–4; terminal segment of abdomen with 4–6

[&]quot;Philopterus rostratus Uchida, 1949: 542". Not Docophorus rostratus Burmeister, 1838.

long anteropleural setae on each side, posteroventral margin with 6–7 long setae on each side, and dorsal margin with 2–4 setae. *Measurements* (n=5, all in mm). DAPW 0.173–0.197; DAPL 0.241–0.281; CL 0.079–0.095; AHW 0.213–0.241; PCHW 0.399–0.424; TW 0.527–0.564; HL 0.620–0.660; PW 0.315–0.333; MW 0.474–0.517; AW 0.542–0.710; TL 1.887–1.990; SGPW 0.270–0.331.

Etymology. The species epithet is formed by the suffix "steno" from Greek = narrow, and "cephalus" from Greek = head, referring to the relatively narrow head of these lice, in comparison with other species of Strigiphilus.

Remarks. Uchida (1949: 542) identified as *Philopterus rostratus* the specimens described here as the new species *Strigiphilus stenocephalus*. As noted above for Uchida's specimens of *S. cursor* and *S. laticephalus*, the year of collection in Uchida's label attached to the specimens of *S. stenocephalus* does not agree with the published year, the label reads "1924" but the paper reads "1923". All other data agree with Uchida's (1949) text, except for the name of a locality, "Tsukurimichi", written in the label but not in the paper. However, Uchida (1949: 542) gave the locality as a place in Aomori Prefecture, and Tsukurimichi belongs to that Prefecture. Therefore, we concluded that the above specimens are those examined and identified by Uchida (1949) as *Philopterus rostratus*.

Japanese host: Otus bakkamoena semitorques Temminck & Schlegel, 1844.

Other hosts: None.

Strigiphilus tuleskovi Balát, 1958

(Fig. 40–44)

Strigiphilus tuleškovi Balát, 1958: 418.

Type host: *Otus scops scops* (Linnaeus, 1758).

Strigiphilus senegalensis Tendeiro, 1963: 75, fig. 24, photos 61-64; Clayton & Price 1984: 347.

Type host: Otus senegalensis senegalensis (Swainson, 1837).

Strigiphilus tuleskovi Balát, 1958; Clayton & Price 1984: 347, figs 13, 34, 56.

Strigiphilus tuleskovi Balát, 1958; Price et al. 2003: 240.

Specimens examined. Ex *Otus sunia japonicus*: $1 \circlearrowleft$, $1 \hookrightarrow$ (slide-mounted), Japan (no other collecting data available) (SEHU); $2 \hookrightarrow$ (preserved in alcohol), same data (SEHU).

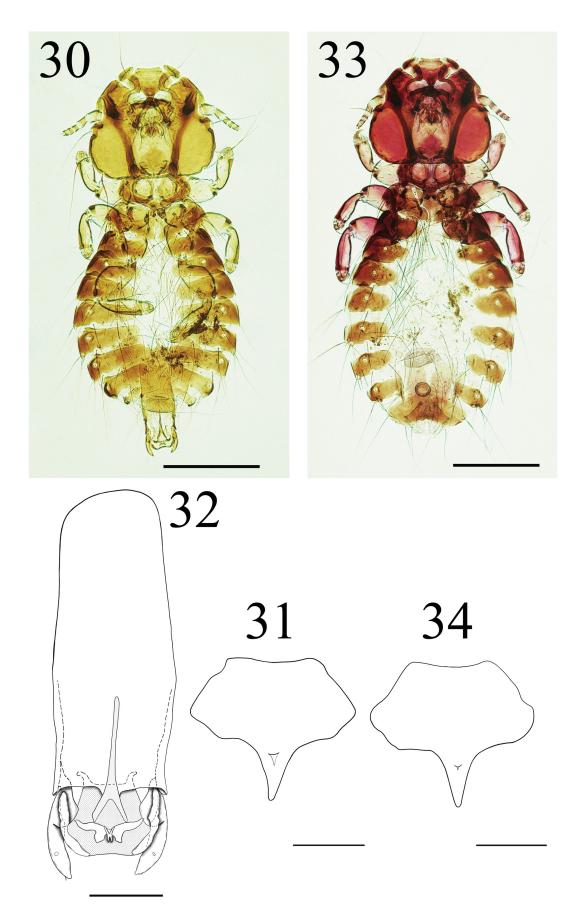
Diagnosis. *Strigiphilus tuleskovi* is morphologically similar to *S. stenocephalus*, but it can be distinguished from the latter species by (1) its smaller head (male: HL < 0.5, TW < 0.43; female: HL < 0.6, TW < 0.48), (2) longer male genitalia compared with total body length, and (3) the configuration of the mesosome of the male genitalia, in particular the shape of the dorsal genitalic plate (Figs 37, 42; see also Clayton & Price 1984, fig. 56).

Japanese host: Otus sunia japonicus Temminck & Schlegel, 1844 (new host association)

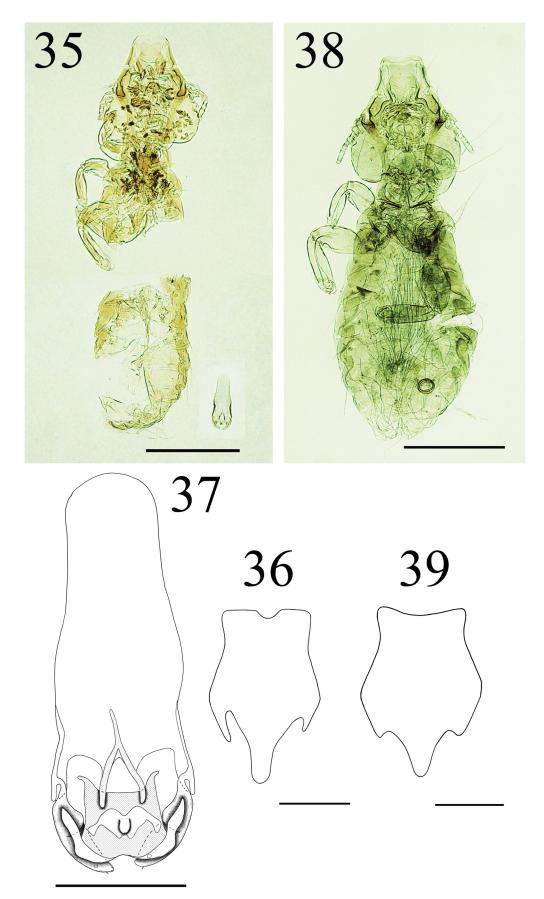
Other hosts: Otus scops scops (Linnaeus, 1758), Otus sunia stictonotus (Sharpe, 1875), Otus senegalensis senegalensis (Swainson, 1837), Otus senegalensis hendersoni (Cassin, 1852).

Key to adults of the Japanese species of Strigiphilus

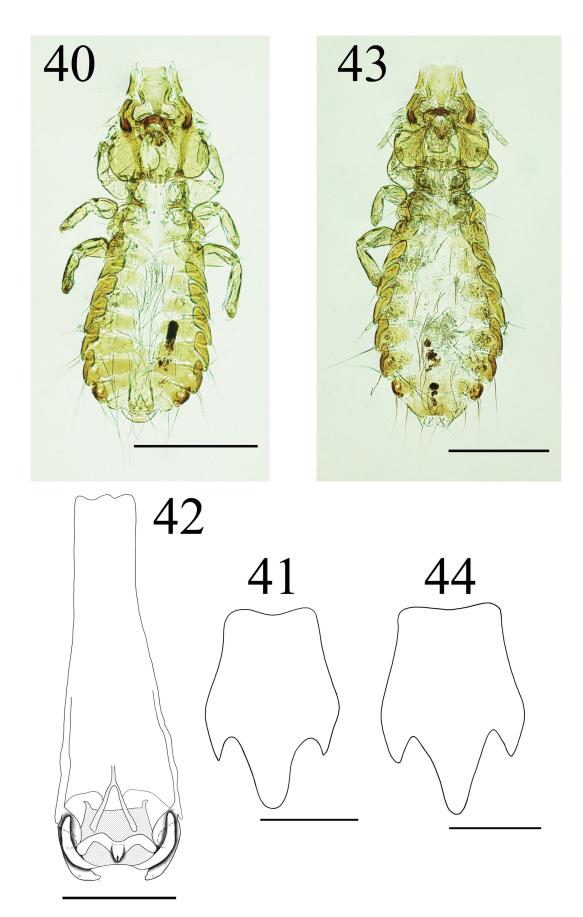
1	Dorsal anterior plate ratio (DAPW/DAPL > 0.8) (Figs 3, 6); antennae sexually dimorphic, first segment of male antennae thick-
	ened and elongated as in Fig. 2 Strigiphilus heterocerus
1'	Dorsal anterior plate ratio (DAPW/DAPL) less than 0.8 (e.g. Figs 36, 39, 41, 44); antennae not sexually dimorphic 2
2	Male genitalia with large mesosome, as in Figs 19, 24, 28; dorsal anterior plate length about half the length of the head
2'	Male genitalia with small mesosome, as in Fig. 9; dorsal anterior plate length less than half the length of the head
3	Abdominal segment III with postspiracular seta; basal apodeme of male genitalia without thickened central prolongation of
	(Figs 9, 14)
3'	Abdominal segment III without long postspiracular seta; basal apodeme of male genitalia with a forked prolongation, not fused
	to penis (Figs 32, 37, 42)
4	Preconal head margin convex (Figs 30, 32)
4'	Preconal head margin concave (Figs 35, 38, 40 43).
5	Male genitalia as in Fig. 42; ratio of male genitalia length to total body length (GL/TL) more than 0.16
	Strigiphilus tuleskovi
5'	Male genitalia as in Fig. 37; ratio of male genitalia length to total body length (GL/TL) less than 0.16
	Strigiphilus stenocephalus



FIGURES 30–34. *Strigiphilus ceblebrachys*: 30, male habitus. 31, male dorsal anterior plate. 32, male genitalia. 33, female habitus. 34, female dorsal anterior plate. Scale bar for 30 and 33: 0.5mm; for 31, 32 and 34: 0.1mm.



FIGURES 35–39. *Strigiphilus stenocephalus*: 35, male habitus. 36, male dorsal anterior plate. 37, male genitalia. 38, female habitus. 39, female dorsal anterior plate. Scale bar for 35 and 38: 0.5mm; for 36, 37 and 39: 0.1mm.



FIGURES 40–44. *Strigiphilus tuleskovi*: 40, male habitus. 41, male dorsal anterior plate. 42, male genitalia. 43, female habitus. 44, female dorsal anterior plate. Scale bar for 40 and 43: 0.5mm; for 41, 42 and 44: 0.1mm.

Discussion

Both Clay (1966b) and Clayton (1990) discussed the apparent lack of host specificity in some species of *Strigiphilus*. Our study of additional louse-host associations of several species of *Strigiphilus* confirm their conclusions. The most significant example is *S. heterogenitalis*, which has been recorded from nine owl species (Price *et al.* 2003) belonging to five genera in three subfamilies of Strigidae (Ninoxinae, Surniinae and Striginae), in addition to two new hosts—*Strix uralensis* and *Otus lempiji pryeri*—in this paper. Another example is *Strigiphilus cursor*, a species primarily parasitic on *Asio flammeus*, but which has now been recorded from *Strix aluco yamadae* in this paper. The geographic distribution of *S. aluco yamadae* and *A. flammeus* overlap in Taiwan. Therefore, it is possible that the host switch of *Strigiphilus cursor* from *A. flammeus* to *S. aluco yamadae* may have occurred in Taiwan. However, Uchida's (1949) record of *S. cursor* (as "*Philopterus cursor* var *laticephalus*") from *Strix aluco yamadae* is still the only one reported in the literature. Hence, it may have been a temporary infestation event, not a permanent host switch. Also, the possibility of a contamination by human agency during louse collection cannot be excluded.

Phoretic behaviour is considered to be one of the major sources of louse host switching, especially among ischnoceran lice (Bartlow *et al.* 2016). In this behaviour, lice utilise louse-flies (Diptera: Hippoboscidae) to move from one host to another. The louse-fly *Ornithoica unicolor* Speiser, 1900 is a parasite of owls, but also of species of other families of birds, such as Accipitridae, Podargidae, Pittidae, Muscicapidae, and Corvidae. However, members of Strigidae are regarded as the breeding hosts of *O. unicolor*, whereas the others are considered to be occasional hosts (Maa, 1966, 1969).

Where two or more owl species are sympatric, hippoboscid flies may facilitate exchange of lice between them, and the owls may even share nesting holes (Clayton 1990). Blagoveshtchensky (1950: 113) recorded *Strigiphilus crenulatus* (Giebel, 1874), a parasite of the owl *Surnia ulula*, on a hippoboscid fly. Although earlier authors did not consider sharing nesting holes as an important means of louse host switching, (e.g. Clay 1949), Johnson et al. (2002) believed that this behaviour may play an important role in host switching.

Mey (1995) sustained that most of the host switching among the species of the *cursitans* species-group is caused by the interspecific killing among sympatric owl species, but he still concluded that most species of *Strigiphilus* are monoxenous and that host-parasite cospeciation patterns are applicable. Mikkola (1976) reported that *Strix aluco* kills and eats smaller raptorial birds, including owls.

From the available data, it does not seem to have been a great degree of cospeciation between owls and their *Strigiphilus* lice, and it is likely that frequent host switches have occurred as discussed above. A molecular phylogenetic study of owl hosts and their *Strigiphilus* lice is needed to determine the extent of host-parasite cospeciation between them.

Acknowledgements

We thank: Satoshi Kamitani (Kyushu University, Fukuoka, Japan) for the loan of Uchida's collection stored in ELKU; Miyako Tsurumi and Yasuko Iwami (Yamashina Institute for Ornithology, Chiba, Japan) for lending us many valuable specimens; and Bradley J. Sinclair (Canadian National Collection of Insects, Ottawa, Ontario, Canada) for information about Hippoboscidae. Also, we thank Ricardo L. Palma (Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand) for his thorough editing and review of the first draft of this paper, and Daniel R. Gustafsson (Guangdong Institute of Applied Biological Resources, Guangzhou, China) for his review of the edited manuscript. This study was partly supported by the Grant-in Aid from JSPS (13740486 and 19H03278) to K.Y.

References

Adam, C. & Daróczi, S.J. (2006) The chewing lice (Phthiraptera: Amblycera, Ischnocera) collected on some Falconiformes and Strigiformes (Aves) from Romania. *Travaux du Muséum National d'Histoire Naturelle "Grigore Antipa"*, 49, 145–168. Balát, F. (1958) Beitrag zur Kenntnis der Mallophagenfauna der bulgarischen Vögel. *Práce Brněnské Základny Československé Akademie Věd*, 30, 397–422.

Bartlow, A.W., Villa, S.M., Thompson, M.W. & Bush, S.E. (2016) Walk or ride? Phoretic behaviour of amblyceran and ischnoceran lice. *International Journal for Parasitology*, 46, 221–227.

- https://doi.org/10.1016/j.ijpara.2016.01.003
- Blagoveshtchensky, D.I. (1950) Mallophaga on birds of Barabinsk Lake (II). *Parasitological team of the Zoological Institute of the USSR Academy of Sciences*, 12, 112–117. [in Russian]
- Burmeister, H. (1838) Mallophaga Nitzsch. *In: Handbuch der Entomologie. Zweite Abteilung. Besondere Entomologie. Zweite Abteilunf. Lauskerfe. Gymnognatha. Zweiter Hälfte. Vulgo Neuroptera.* Theod. Chr. Fried Enslin, Berlin, pp. 418–443.
- Clay, T. (1949) Some problems in the evolution of a group of ectoparasites. *Evolution*, 3, 279–299. https://doi.org/10.1111/j.1558-5646.1949.tb00030.x
- Clay, T. (1966a) The species of *Strigiphilus* (Mallophaga: Philopteridae) parasitic on the barn owls, *Tyto* (Tytonidae). *Journal of the Entomological Society of Queensland*, 5, 10–17. https://doi.org/10.1111/j.1440-6055.1966.tb00671.x
- Clay, T. (1966b) A new species of Strigiphilus (Philopteridae: Mallophaga). Pacific Insects, 8 (4), 835–847.
- Clayton, D.H. (1990) Host specificity of *Strigiphilus* owl lice (Ischnocera: Philopteridae), with the description of new species and host associations. *Journal of Medical Entomology*, 27 (3), 257–265. https://doi.org/10.1093/jmedent/27.3.257
- Clayton, D.H. & Price, R.D. (1984) Taxonomy of the *Strigiphilus cursitans* group (Ischnocera: Philopteridae), parasites of owls (Strigiformes). *Annals of the Entomological Society of America*, 77 (4), 340–363. https://doi.org/10.1093/aesa/77.4.340
- Denny, H. (1842) Monographia Anoplurorum Britanniae or, an essay on the British species of parasitic insects belonging to the order of Anoplura of Leach, with the modern divisions of the genera according to the views of Leach, Nitzsch, and Burmeister, with highly magnified figures of each species. Henry G. Bohn, London, xxiv + 262 pp., 26 pls. https://doi.org/10.5962/bhl.title.137104
- Denny, H. (1852) List of British Anoplura. *In: Gray, J.E., List of specimens of British animals in the collection of the British Museum. Vol. 11*. The Trustees of the British Museum, London, pp. 1–51.
- Eichler, W. (1949) Die Eulenfederlinge. Beiträge zur Taxonomischen Zoologie, 1, 7–22.
- Emerson, K.C & Elbel, R.E. (1957) New species and records of *Strigiphilus* (Philopteridae: Mallophaga) from Thailand. *Proceedings of the Biological Society of Washington*, 70,195–200.
- Grube, E. (1851) Beschreibung der auf A. Th. Von Middendorff's Sibirische Reise gesammelten. Parasiten. *In*: von Middendorff, A.T. (Ed.), *Reise in den äußersten Norden und Osten Sibiriens während der Jahre 1843–1844, St Petersburg*, Zoologie, 2 (1), pp. 467–497, 516, pls. 31–32.
- Haeckel, E. (1896) Systematische Phylogenie. 2. Theil. Systematische Phylogenie der wirbellosen Thiere (Invertebrata). Verlag von Georg Reimer, Berlin, 720 pp. https://doi.org/10.1515/9783111443935
- Hafner, M.S., Sudman, P.D., Villablanca, F.X., Spradling, T.A., Demastes, J.W. & Nadler, S.A. (1994) Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science*, 265, 1087–1090. https://doi.org/10.1126/science.8066445
- Hopkins, G.H.E. & Clay, T. (1952) A check list of the genera & species of Mallophaga. Trustees of the British Museum, London, 362 pp.
 - https://doi.org/10.5962/bhl.title.118844
- Hughes, J., Kennedy, M., Johnson, K.P., Palma, R.L. & Page, R.D.M. (2007) Multiple cophylogenetic analyses reveal frequent cospeciation between pelecaniform birds and *Pectinopygus* lice. *Systematic Biology*, 56 (2), 232–251. https://doi.org/10.1080/10635150701311370
- Johnson, K.P., Adams, R.J. & Clayton, D.H. (2002) The phylogeny of the louse genus *Brueelia* does not reflect host phylogeny. *Biological Journal of the Linnean Society*, 77, 233–247. https://doi.org/10.1046/j.1095-8312.2002.00107.x
- Kellogg, V.L. (1896) New Mallophaga, I,—with special reference to a collection made from maritime birds of the Bay of Monterey, California. *Proceedings of the California Academy of Sciences*, Series 2, 6, 31–168, 14 pls.
- Maa, T.C. (1966) The genus Ornithoica Rondani (Diptera: Hippoboscidae). Pacific Insects Monograph, 10, 10–124.
- Maa, T.C. (1969) A revised checklist and concise host index of Hippoboscidae (Diptera). *Pacific Insects Monograph*, 20, 261–299.
- Mey, E. (1995) Wiederbeschreibung des Sperlingskauz-Federlings *Strigiphilus splendens* (Insecta, Phthiraptera, Ischnocera) und parasitophyletische Anmerkungen über die Eulen (Strigiformes). *Anzeiger des Vereins Thüringer Ornithologen*, 2, 193–205.
- Mikkola, H. (1976) Owls killing and killed by other owls and raptors in Europe. British Birds, 69, 144–154.
- Mjöberg, E. (1910) Studien über Mallophagen und Anopluren. *Arkiv för Zoologi*, 6 (13), 1–296, 5 pls. https://doi.org/10.5962/bhl.part.26907
- Ornithological Society of Japan (2012) *Check-list of Japanese birds* 7th revised edition. The Ornithological Society of Japan, Sanda, 438 pp.
- Page, R.D. M., Lee, P.L., Becher, S.A., Griffiths, R. & Clayton, D.H. (1998) A different tempo of mitochondrial evolution in birds and their parasitic lice. *Molecular Phylogenetics and Evolution*, 9, 276–293. https://doi.org/10.1006/mpev.1997.0458
- Piaget, E. (1880) Les Pédiculines. Essai Monographique. Vols. 1–2. E.J. Brill, Leide, xxxix + 714 pp., 56 pls.

- Price, R.D., Hellenthal, R.A. & Palma, R.L. (2003) World checklist of chewing lice with host associations and keys to families and genera. *In*: Price, R.D., Hellenthal, R.A., Palma, R.L., Johnson, K.P. & Clayton, D.H. (Eds.), *The Chewing lice: world checklist and biological overview. Illinois Natural History Survey Special Publication 24*. Illinois Natural History Survey, Champaign, Illinois, pp. i–x + 1–501.
- Smith, V.S. (2001) Avian louse phylogeny (Phthiraptera: Ischnocera): A cladistic study based on morphology. *Zoological Journal of the Linnean Society*, 132 (1), 81–144. https://doi.org/10.1111/j.1096-3642.2001.tb02272.x
- Tendeiro, J. (1963) Études sur les mallophages. Observations sur des Ischnocera africains avec description de 12 espèces et 2 sous- espèces nouvelles. *Boletim Cultural da Guiné Portuguesa*, 18, 13–106.
- Uchida, S. (1948) Studies on the biting-lice (Mallophaga) of Japan and adjacent territories (suborder Ischnocera Pt. I). *The Japanese Medical Journal*, 1 (4), 303–326. https://doi.org/10.7883/yoken1948.1.303
- Uchida, S. (1949) Studies on the biting-lice (Mallophaga) of Japan and adjacent territories (suborder Ischnocera Pt. II). *The Japanese Medical Journal*, 1 (6), 535–556. https://doi.org/10.7883/yoken1948.1.535
- Złotorzycka, J. (1974) Revision der europäischen Strigiphilini (Mallophaga, Strigiphilinae). *Polskie Pismo Entomologiczne*, 44, 319–358.